Among- and within-tributary responses of riverine fish assemblages to habitat features[1]

Yorick Reyjol, Marco A. Rodríguez, Nathalie Dubuc, Pierre Magnan, and Réjean Fortin

Abstract: We quantified fish abundance and environmental variables at 170 sites distributed among 11 tributaries of the Ottawa River, Quebec, Canada, to assess the relative importance of among- and within-tributary variation in riverine fish assemblages. Additionally, we determined (*i*) which environmental variables were most strongly associated with each type of variation and (*ii*) whether ecomorphological traits in fish assemblages were predictably related to environmental gradients. Partitioning of variation by means of partial ordination indicated that assemblages were less variable among (38.7% of the total variation) than within (61.3%) tributaries. Water transparency singly accounted for 33.3% of the variation among tributaries, whereas macrophyte cover and river width jointly accounted for 8.3% of the variation within tributaries. These results suggests that differences in habitat features among tributaries may account for a substantial fraction of the predictable variation in assemblage structure at the watershed scale, an aspect not emphasized in previous studies of riverine fish assemblages. Mixed regression analyses relating ecomorphological traits to environmental variables showed that the environmental variables most strongly associated with assemblage structure were significantly related to traits associated with predator avoidance or foraging efficiency.

Résumé : Les communautés de poissons et des variables environnementales ont été quantifiées à 170 sites répartis le long de 11 affluents de la rivière des Outaouais (Québec, Canada), afin de déterminer l'importance relative de la variation inter- et intra-affluents dans la structuration des communautés. De plus, nous avons déterminé (*i*) quelles variables environnementales étaient le plus fortement associées à chaque type de variation et (*ii*) si les traits écomorphologiques caractérisant les communautés étaient liés de façon prévisible aux gradients environnementaux inter- et intra-affluents. La partition de la variation par ordination partielle a mis en évidence que les communautés étaient moins variables entre elles (38,7 % de la variation totale) qu'au sein (61,3 %) des affluents. La transparence de l'eau expliquait à elle seule 33,3 % de la variation entre les affluents, tandis que le couvert de macrophytes et la largeur de la rivière expliquaient conjointement 8,3 % de la variation au sein des affluents. Ces résultats suggèrent que des différences dans les caractéristiques de l'habitat entre les affluents pourraient jouer un rôle prépondérant dans la structuration des communautés de poissons de rivière à l'échelle du bassin versant, un aspect qui n'a pas été mis en lumière dans les études précédentes. Des analyses de régression mixte mettant en rélation les traits écomorphologiques et les variables environnementales ont montré que les variables environnementales associées à la structuration des communautés étaient significativement reliées à des traits liés à l'évitement des prédateurs et à l'efficacité de l'alimentation.

Introduction

Variation in riverine fish assemblages within a watershed can be conceptually split into among- and within-tributary components. Apportioning assemblage variation to among- and within-tributary components and identifying the environmental determinants of both types of variation may have important implications for riverine fish ecology, yet very few studies have specifically quantified the relative importance of these two components (e.g., Humpl and Pivnička 2006). For example, when species–environment relationships are stronger among than within tributaries, differential colonization of tributaries from the river mainstem (including both immigration to the tributary and subsequent establishment in it) may be driven by habitat preferences of the species in the regional pool. Assemblage structure and local adaptations by individuals may then be primarily regulated by transversal (i.e., among-tributary) processes. Exchanges between tributaries and the river mainstem can be of great consequence to the organization of fish assemblages at the local and watershed scales, as suggested by the network dynamics hypothesis (Benda et al. 2004; Lowe et al.

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[1] Contribution of the Group for Interuniversity Research in Limnology (GRIL). We dedicate this paper to the memory of our colleague Réjean Fortin.

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2006). This hypothesis views rivers as networks of channels and confluences and proposes that the physical characteristics at tributary junctions can intensify spatial and temporal habitat heterogeneity at those points, thereby influencing the productivity and distribution of aquatic organisms (e.g., by generating biological hotspots). The importance of exchanges between tributaries and the mainstem is also supported by evidence from field studies showing that tributaries located lower in a drainage network have greater species richness than similarly sized streams located in the headwaters of the network (Osborne and Wiley 1992) and that mainstem species richness tends to increase downstream of tributary confluences (Cox Fernandes et al. 2004).

In contrast, when species–environment relationships are stronger within than among tributaries, species from the river mainstem may not preferentially colonize specific tributaries, and assemblage structure at the watershed scale, as well as local adaptations by individuals, should be related mostly to longitudinal processes (Rahel and Hubert 1991; Reyjol et al. 2001; Grenouillet et al. 2004). Change in fish assemblage structure within tributaries is often predictably related to longitudinal gradients in environmental variables such as water temperature, water transparency, current velocity, dissolved oxygen concentration, and substratum size (e.g., Ostrand and Wilde 2002; Li and Gelwick 2005; Humpl and Pivnička 2006). Elucidating the rules underlying fish assemblage organization at the watershed scale can contribute to our understanding of evolutionary processes, because watersheds can be biogeographical stages for speciation and extinction events (Reyjol et al. 2007).

Aquatic ecologists are interested in relating not only the taxonomic composition of fish assemblages, but also their traits composition (i.e., the relative representation of key biological or morphological attributes) to environmental variation (Goldstein and Meador 2004; Hoeinghaus et al. 2006). Studies examining relationships between morphology and habitat often focus on feeding ecology in the context of resource partitioning (e.g., Winemiller 1991); relatively few studies have examined the responses of morphological traits of riverine fish species to environmental variation (e.g., Gatz 1981). However, morphological traits have been shown to respond to both hydrological and geomorphic gradients (Lamouroux et al. 2002; Willis et al. 2005) and to vary in relation to river size (i.e., from small streams to large rivers; Goldstein and Meador 2004).

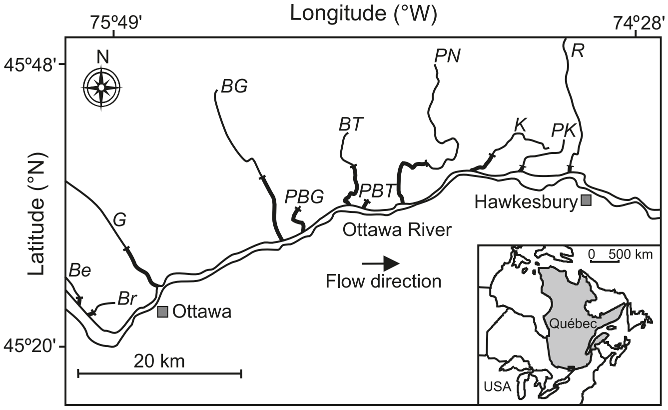
The objectives of the present study were to determine (*i*) the relative importance of among- and within-tributary variation in fish assemblages of the Ottawa River, Quebec, Canada; (*ii*) which environmental variables were most strongly associated with each type of variation; and (*iii*) whether ecomorphological traits of fish assemblages were predictably related to environmental gradients both among and within tributaries.

Materials and methods

Study area and sampling methods

Fish samples and environmental measurements were collected during the summer in 1995 (31 July – 8 August) and 1996 (8–23 August) from 11 tributaries spread across a 70 km stretch of the Ottawa River (watershed area: 146 000 km^2; mean discharge: 1937 m^3·s^{-1}) (Fig. 1). Along this stretch, the alluvial plain of the Ottawa River is generally narrow (several hundred metres to several kilometres); its sedimentary deposits are rich in clay and silt. The tributaries originate in the Canadian Shield and run through it before traversing the alluvial plain and reaching the Ottawa River. In the reaches running through the shield, the tributaries have clear waters and streambeds characterized by coarse substrata, but transparency declines as the tributaries enter the plain. The extent of this decline varies among tributaries because the decline arises from loading of fine inorganic sediment, which in turn depends on the length of the trajectory through the plain (H. Fournier, Ministère des Ressources naturelles et de la Faune, Direction de l'aménagement de la faune de l'Outaouais, Faune Québec, 98 rue Lois, Gatineau, QC J8Y 3R7, Canada, personal communication).

Fig. 1. Tributaries of the Ottawa River included in the present study: Be, Bélisle Brook; Br, Breckenridge Brook; G, Gatineau River; BG, Blanche à Gatineau River; PBG, Petite Blanche à Gatineau River; BT, Blanche à Thurso River; PBT, Petite Blanche à Thurso River; PN, Petite Nation River; K, Kinonge River; PK, Petite Kinonge River; R, Rouge River. In each tributary, samples were collected at equidistant points along the reaches (thick tracing) between the Ottawa River and the first insurmountable barrier (hatch mark).



Within each tributary, systematic sampling was conducted at sites spaced uniformly between the Ottawa River and the first barrier judged to be insurmountable to fish. Barriers were generally falls or short rapids associated with an escarpment several metres high at the junction of the river plain with the Canadian Shield. In all, 170 sites were sampled, 10 in each of the five tributaries for which the barrier was <1 km away from the Ottawa River and 20 in each of the six remaining tributaries (Table 1). Fish were collected at the selected sites using a beach seine (length: 20.3 m; height: 3.7 m at the center and 1.8 m at the extremities; 12.7 mm stretch mesh). At each site, one seine haul was conducted over a semicircular area (~160 m^2) free of obstacles to effective seining (e.g., steep slope, snags). Fish were counted and identified to species. Nine environmental variables were measured (Table 2): river width, bank slope, water transparency (Secchi depth), mean current velocity (Gurley Price current meter), dissolved oxygen concentration (YSI 54 A), pH (Brinkmann E604), macrophyte cover (bed width), macrophyte richness (number of taxa in the

Table 1. Code, number of sampling sites, and distance between the Ottawa River and the first barrier on the tributary for the 11 tributaries of the Ottawa River included in this study.

Tributary	Code	No. of sites	Distance (m)
Bélisle	Be	10	630
Blanche à Gatineau	BG	20	7700
Blanche à Thurso	BT	20	6200
Breckenridge	Br	10	600
Gatineau	G	20	5900
Kinonge	K	20	3100
Petite Blanche à Gatineau	PBG	20	3000
Petite Blanche à Thurso	PBT	10	790
Petite Kinonge	PK	10	820
Petite Nation	PN	20	8200
Rouge	R	10	730

Table 2. Median and upper and lower 5% percentiles for nine environmental variables measured at 170 sites.

Environmental variable	Median (5%–95%)	ICC
River width (m)	26.5 (8.5–260.0)	0.85
Bank slope (°)	13 (2–25)	0.18
Water transparency (cm)	67 (18–293)	0.91
Mean current velocity ($cm \cdot s^{-1}$)	<1.5 (<1.5–7.3)	0.45
DOC (ppm)	7.9 (4.6–8.5)	0.95
pH	7.8 (6.7–8.4)	0.93
Macrophyte cover (m)	3.0 (0.0–19.0)	0.27
Macrophyte richness (no. of taxa)	3 (0–8)	0.31
Substratum size (index)	1 (1–2)	0.17

Note: The intraclass correlation coefficient (ICC), measured as the ratio of among-tributary variation to total variation (among- plus within-tributary), is also reported for each variable. DOC, dissolved organic carbon.

seined area; resolution to species or genus), and a substratum size index, defined as the most common size class in the seined area, as determined by visual and tactile examination (size classes were coded as scores ranging from 1 to 6 for particle diameters with boundaries at 1, 3, 17, 65, and 265 mm; modified from Bovee 1986). River width and macrophyte cover were measured along a transect perpendicular to flow, corresponding to a cross-section over the whole river width. Water transparency, mean current velocity, dissolved oxygen concentration, and pH were measured at the centre of the transect. Mean current velocity was measured at 0.6 times water depth for depths <1 m and at 0.2, 0.6, and 0.8 times water depth for depths >1 m (Bovee 1986). In the latter case, mean current velocity was calculated as $V_{\mathrm{mean}} = (V_{0.2} + 2V_{0.6} + V_{0.8})\,0.25$. Bank slope was calculated from the horizontal distance, measured transversally to flow, between the shoreline and the point at which water depth attained 3 m. For two shallow tributaries (Bélisle Brook and Breckenridge Brook), a depth of 0.5 m was used instead of 3 m.

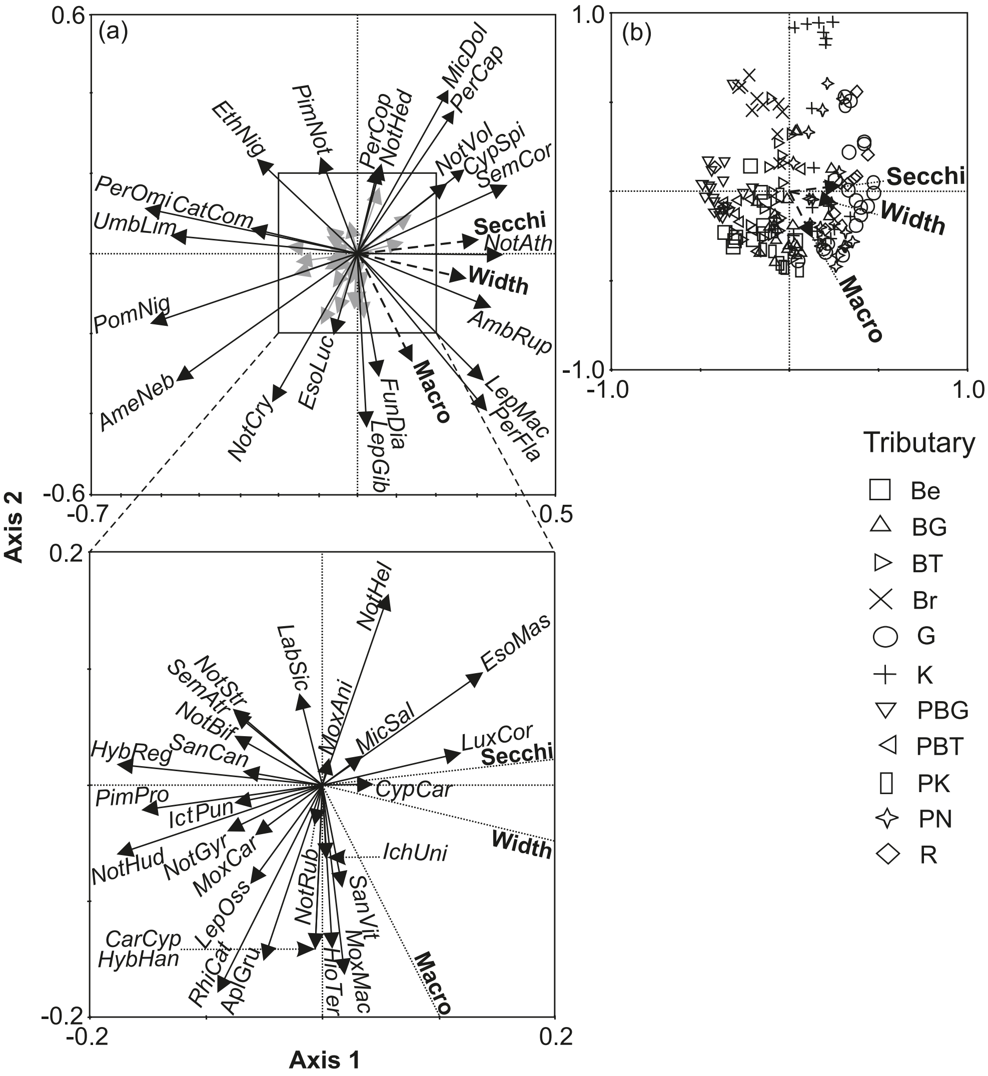
Partitioning of variation and species–environment relationships

We conducted three separate ordination analyses: a full analysis including both among- and within-tributary variation, equivalent to a conventional ordination; and two partial analyses, one focusing on among-tributary variation and the other on within-tributary variation. In the full analysis, variation in assemblage structure was examined in relation to a set of environmental predictors, without using covariates. The partial analyses were used to apportion the total variation in fish assemblage structure into among- and within-tributary components and to quantify, for each component, the variation explained by the environmental variables. Three sets of covariates were used in the partial analyses (see simplified example in Appendix A, Table A1). The first set of covariates, **T**, was structured as a 170 × 10 (rows × columns) matrix of effects coding that assigned each of the 170 samples to one of the 11 tributaries (only 10 variables are required to distinguish among 11 tributaries). Covariate set **T** accounts for variation among tributaries. The second set of covariates, **S**, was structured as a 170 × 19 matrix of effects coding that assigned each of the samples to a specific site within the tributary (19 variables are required to distinguish among 20 sites). Covariate set **S** accounts for additive patterns of within-tributary variation that are shared by all tributaries. The third set of covariates was obtained by first calculating the column-by-column product of **T** and **S** to yield a 170 × 190 matrix (command matrix.model in the R software, v. 2.3.1; R Development Core Team 2006) and then reducing this matrix to a 170 × 140 matrix by eliminating 50 collinear variables (collinear variables are dropped automatically by most linear modelling software; e.g., command lm in the R software). The resulting matrix, **T**·**S**, coded for the interaction between tributaries and sites. Covariate set **T**·**S** accounts for the residual (nonadditive) within-tributary variation that is not shared among tributaries and reflects site-specific deviations from the additive pattern common to all tributaries. The coding used ensures that covariates set **T** is linearly independent of sets **S** and **T**·**S** combined; furthermore, sets **T**, **S**, and **T**·**S** jointly exhaust the variation in assemblage structure. In this context, the interaction term **T**·**S** is used jointly with term **S** solely as a quantitative device to extract all of the within-tributary variation. We were not interested in an ecological interpretation of the interaction term, because this term reflects idiosyncratic variation associated with site-specific characteristics that do not generalize across tributaries.

The total variation in fish assemblage structure was partitioned into an among-tributary component, obtained as the variation accounted for by set **T**, and a within-tributary component, calculated as the total variation minus the among-tributary variation. Equivalently, the within-tributary component could have been obtained directly as the variation jointly accounted for by sets **S** and **T**·**S**, and the among-tributary component could then be calculated as the total variation minus the within-tributary variation.

The variation explained by the environmental variables among tributaries and within tributaries was quantified in two separate analyses. In the first analysis, set **T** was used as covariates in a partial ordination to statistically remove differences among tributaries, thereby focusing on environmental effects related solely to within-tributary variation in assemblage structure. This analysis included a set of envi-

Fig. 2. (*a*) Species and (*b*) sites ordination plots for the full redundancy analysis (RDA). The two ordination axes (axis 1: $P = 0.005$; axis 2: $P = 0.020$) jointly account for 20.4% of the total variation in assemblage structure. Species codes are given in Appendix B, Table B1. Be, Bélisle Brook; Br, Breckenridge Brook; G, Gatineau River; BG, Blanche à Gatineau River; PBG, Petite Blanche à Gatineau River; BT, Blanche à Thurso River; PBT, Petite Blanche à Thurso River; PN, Petite Nation River; K, Kinonge River; PK, Petite Kinonge River; R, Rouge River; Secchi, water transparency; Macro, macrophyte cover; Width, river width.



ronmental variables as predictors in addition to set **T** as covariates. In the second analysis, sets **S** and **T·S** were used jointly as covariates in a partial ordination to statistically remove the variation within tributaries and focus on environmental effects related solely to among-tributary variation in assemblage structure. This analysis included a set of environmental variables as predictors in addition to sets **S** and **T·S** used jointly as covariates.

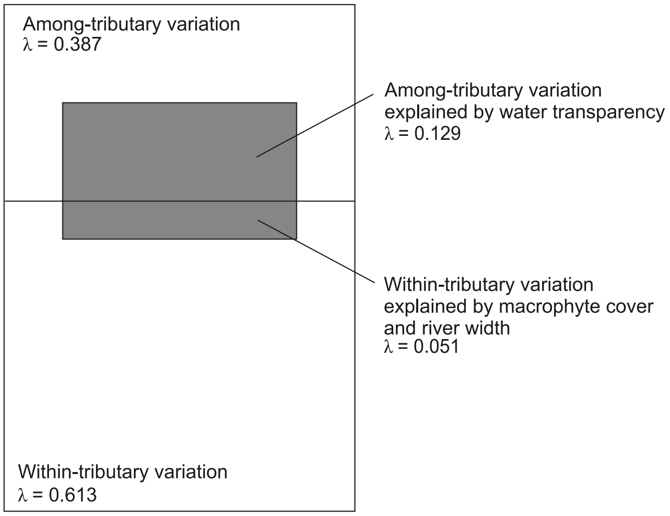
We based all ordinations on redundancy analyses (RDA) and partial redundancy analyses instead of the more commonly used canonical correspondence analyses (CCA). CCA did not allow us to unambiguously partition the variation, presumably because rows in the design matrix in CCA are assigned different weights, and therefore linearly independent covariates do not remain independent after weights are applied. In contrast, no such weighting is used in RDA. We used a Hellinger transformation of species abundances because a preliminary detrended correspondence analysis yielded a relatively long gradient (3.97 standard deviations in the sample scores). The Hellinger transformation renders RDA effective as an alternative to CCA for the analysis of species abundances when gradients are long (Legendre and Gallagher 2001). In the ordination analyses involving environmental variables, a forward selection procedure based on a nominal cut-off point ($P = 0.05$) was used to determine which of the nine environmental variables measured were useful predictors of assemblage structure (program CANOCO, version 4.5; ter Braak and Šmilauer 2002). Environmental variables not retained by the selection procedure were not included in the ordinations. Statistical significance was determined by Monte Carlo tests (1000 permutations) for the individual predictors, the sum of all eigenvalues, and the ordination axes. The nested structure of samples was maintained during resampling by use of within-block permutations (i.e., random reshuffling was unrestricted among tributaries with the same number of sites but was restricted for sites within tributaries).

Influence of environmental variables on ecomorphological traits

Ecomorphological traits potentially linked to ecology and behaviour were obtained for the fish species in this study (Appendix B, Table B1) from published sources, following an approach similar to those of Poff and Allan (1995) and Lamouroux et al. (2002). Image analysis software (SigmaScan Pro, version 5.0; Systat Software Inc., Point Richmond, California) was used to measure six quantitative traits from illustrations in Scott and Crossman (1985): relative eye diameter (standardized by total length; EyeDiam), relative length of the pectoral fin (standardized by total length; PectLength), relative insertion height of the pectoral fin (ratio of insertion height to body depth at insertion site; PectHeight), dorsal insertion distance (snout to anterior insertion of dorsal fin, standardized by total length; DorsDist), shape factor (ratio of total length to maximum body depth; ShapeF), swimming factor (ratio of minimum depth of caudal peduncle to maximum depth of caudal fin; SwimF). Five qualitative traits were coded using information in Scott and Crossman (1985), Froese and Pauly (2006), and the Fish ID collection (Lyons et al. 2006): mouth position (Mouth: 0, inferior; 1, terminal or subterminal; 2, superior); four variables denoted presence or absence of a trait (binary coding): barbels (Barbels), mottled or vertical stripe patterns on the body (Pattern), silvery body coloration (Silver), and lateral stripe (LatStripe). Analyses of PectHeight and SwimF did not include the silver lamprey (*Ichthyomyzon unicuspis*), which lacks pectoral fins and a distinct caudal peduncle. For each site, a mean value was obtained for each of the traits by averaging across all individuals captured at the site, irrespective of species identity.

In nested sampling designs, units within a group tend to be more similar to other units in the same group than to units in other groups (i.e., there is substantial intraclass correlation); thus, individual observations are not entirely independent as required by conventional regression models. To account for the nesting of sites within tributaries, linear mixed regressions (nlme package version 3.1-79 of the R software; R Development Core Team 2006), which account for intraclass correlation by means of random effects for the parameters, were used to assess the relationship between each ecomorphological trait and the environmental variables retained in the partial ordination analyses. A parametric bootstrap (1000 iterations) was used to determine whether random effects were needed for the slope and intercept (Faraway 2006). Because several environmental variables were tested at once in each model, their effects were assessed through Wald tests adjusted by the Benjamini–Hochberg (false discovery rate) procedure (García 2004). The intraclass correlation coefficient (ICC), which measures the proportion of the total variation that is among groups (Faraway 2006), was used to quantify the relative importance of among- and within-tributary variation for each of the environmental variables. The ICC can range from 0 (all variation is within tributaries) to 1 (all variation is among tributaries). Linear mixed regressions were also used to assess longitudinal variation in environmental variables selected in the partial ordinations. In all analyses, logarithmic (river width, water transparency, mean current velocity, macrophyte cover) or square-root (bank slope) transformations were used to reduce the influence of extreme points and better fit the assumptions of linearity, normality, and homoscedasticity.

Fig. 3. Venn diagram illustrating the partitioning of total and explained variation in fish assemblages among and within tributaries. The ordination eigenvalues (λ) reflect the variation associated with each component, expressed as a fraction of the total variation (1.0).

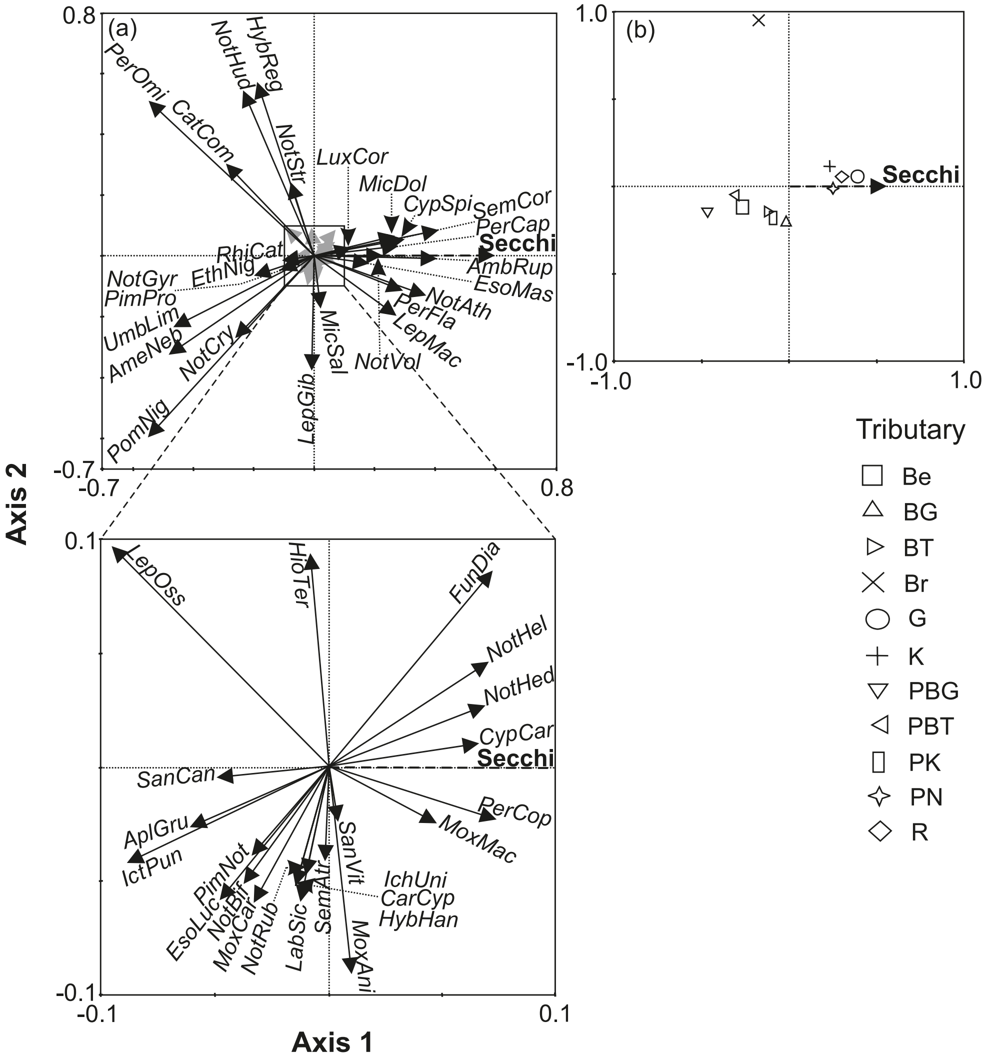


Results

In the full ordination analysis, three of the nine environmental variables initially considered were retained by the forward selection procedure: water transparency (P = 0.002), macrophyte cover (P = 0.001), and river width (P = 0.007). The first ordination axis reflected a gradient in water transparency and river width, whereas the second axis was associated with a gradient in macrophyte cover (Fig. 2*a*). Species associated with water transparency and river width included several small cyprinids (emerald shiner (*Notropis atherinoides*), spotfin shiner (*Cyprinella spiloptera*), mimic shiner (*Notropis volucellus*), fallfish (*Semotilus corporalis*)), rock bass (*Ambloplites rupestris*), bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*) (positive associations); and trout-perch (*Percopsis omiscomaycus*), black crappie (*Pomoxis nigromaculatus*), central mudminnow (*Umbra limi*), and brown bullhead (*Ameiurus nebulosus*) (negative associations). Species associated with macrophyte cover included bluegill, pumpkinseed (*Lepomis gibbosus*), yellow perch, banded killifish (*Fundulus diaphanus*) (positive associations); and bluntnose minnow (*Pimephales notatus*), and johnny darter (*Etheostoma nigrum*) (negative associations). The scatter on the ordination plot for sites (Fig. 2*b*) reflects variation both among and within tributaries.

Partitioning of the total variation showed that assemblages were less variable among (38.7% of the total variation) than within tributaries (61.3%) (Fig. 3). In the partial ordination analysis focusing on variation among tributaries (**S** and **T·S** as covariates), water transparency was the only predictor re-

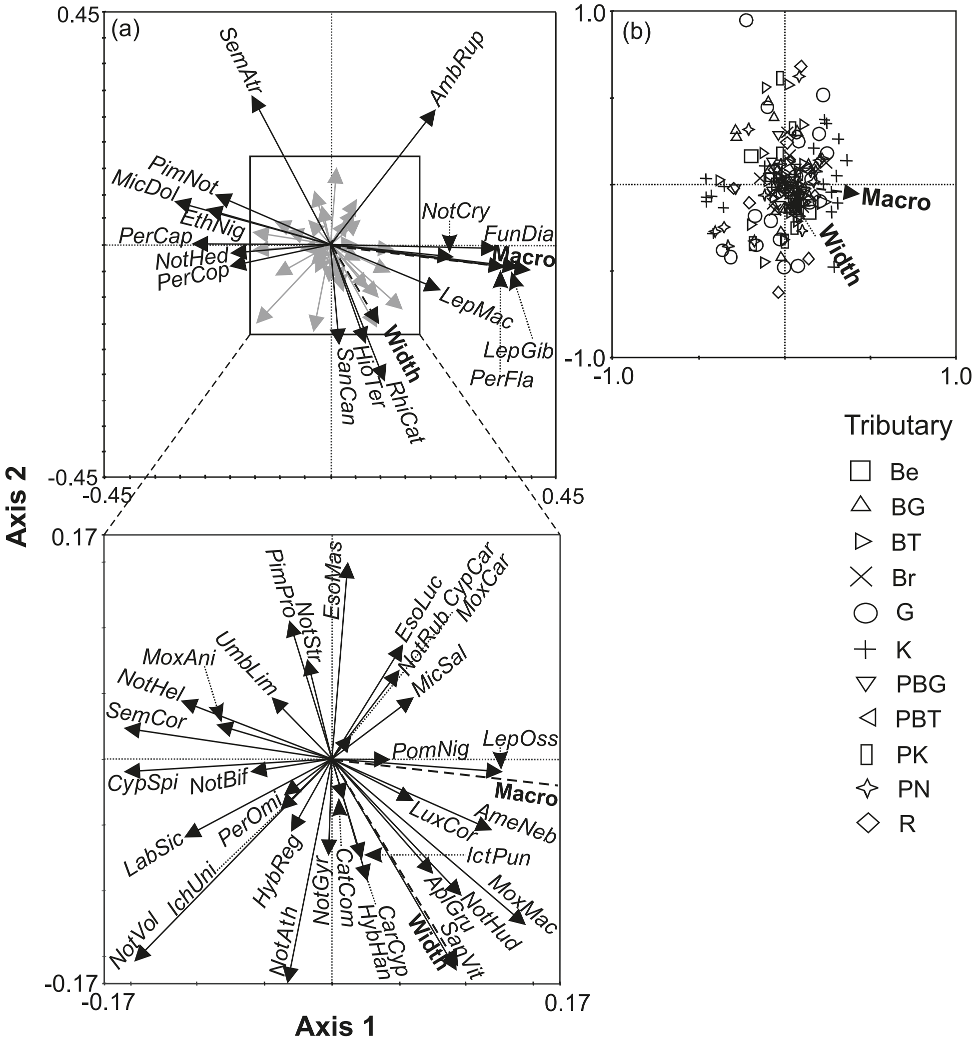
Fig. 4. (*a*) Species and (*b*) sites ordination plots for the partial redundancy analysis (RDA) focusing on among-tributary variation. The first ordination axis (P = 0.003) accounts for 33.3% of the among-tributary variation in assemblage structure; the second axis represents residual variation not accounted for by water transparency. Species codes are given in Appendix B, Table B1. Be, Bélisle Brook; Br, Breckenridge Brook; G, Gatineau River; BG, Blanche à Gatineau River; PBG, Petite Blanche à Gatineau River; BT, Blanche à Thurso River; PBT, Petite Blanche à Thurso River; PN, Petite Nation River; K, Kinonge River; PK, Petite Kinonge River; R, Rouge River; Secchi, water transparency.



tained by the forward selection procedure (P = 0.003) (Fig. 4*a*). Water transparency explained 12.9% of the total variation (Fig. 3) (i.e., 33.3% of the variation among tributaries). Species associated with water transparency included emerald shiner, spotfin shiner, fallfish, bluegill, rock bass, yellow perch, and logperch (*Percina caprodes*) (positive associations); and trout-perch, black crappie, central mudminnow, and brown bullhead (negative associations). Because in this analysis all within-tributary variation has been extracted by the covariates, in the ordination plot for sites (Fig. 4*b*), all sites within a tributary are located at the centroid specific to that tributary. Therefore, the scatter along axis 1 reflects solely variation among tributaries (axis 2 reflects only residual variation because there is a single environmental predictor in this analysis).

In the partial ordination analysis focusing on variation within tributaries (**T** as covariates), two environmental variables were selected by the forward selection procedure: macrophyte cover (P = 0.002) and river width (P = 0.002) (Fig. 5*a*). Macrophyte cover and river width jointly explained 5.1% of the total variation (Fig. 3) (i.e., 8.3% of the variation within tributaries). The first axis was associated with a gradient in macrophyte cover, whereas the second axis was associated with variation in river width. Both macrophyte cover and river width declined longitudinally as a function of distance to the Ottawa River (Fig. 6; mixed regression $P < 0.001$ for both relationships); however, distance to the Ottawa River itself was not significantly related to assemblage structure when it was included as a potential predictor in the ordination analyses. Neither regression required random effects for the slope, indicating that the effect of distance was similar across tributaries. Species associated with macrophyte cover included bluegill, pumpkinseed, yellow perch, banded killifish, and golden shiner (*Notemigonus crysoleucas*) (positive associations); and bluntnose minnow, smallmouth bass (*Micropterus dolomieu*), logperch, and johnny darter (negative associations). The species most strongly associated with river width were longnose dace

Fig. 5. (*a*) Species and (*b*) sites ordination plots for the partial redundancy analysis (RDA) focusing on within-tributary variation. The two ordination axes (axis 1: $P = 0.002$; axis 2: $P = 0.009$) jointly account for 8.3% of the within-tributary variation in assemblage structure. Species codes are given in Appendix B, Table B1. Be, Bélisle Brook; Br, Breckenridge Brook; G, Gatineau River; BG, Blanche à Gatineau River; PBG, Petite Blanche à Gatineau River; BT, Blanche à Thurso River; PBT, Petite Blanche à Thurso River; PN, Petite Nation River; K, Kinonge River; PK, Petite Kinonge River; R, Rouge River; Macro, macrophyte cover; Width, river width.



(*Rhinichthys cataractae*) (positive association) and creek chub (*Semotilus atromaculatus*) (negative association). Because in this analysis all among-tributary variation has been extracted by the covariates, in the ordination plot for sites (Fig. 5*b*), all tributaries have a common centroid at the origin. Therefore, the scatter reflects solely variation within tributaries, about the common centroid.

Marked differences between the full analysis and the partial analyses were found for some species responses. For example, rock bass showed an association with water transparency and river width in the full analysis (Fig. 2*a*), but the association with river width was no longer visible in the partial analysis focusing on within-tributary variation (Fig. 5*a*). However, the relationship with water transparency was still detectable in the partial analysis focusing on among-tributary variation (Fig. 4*a*).

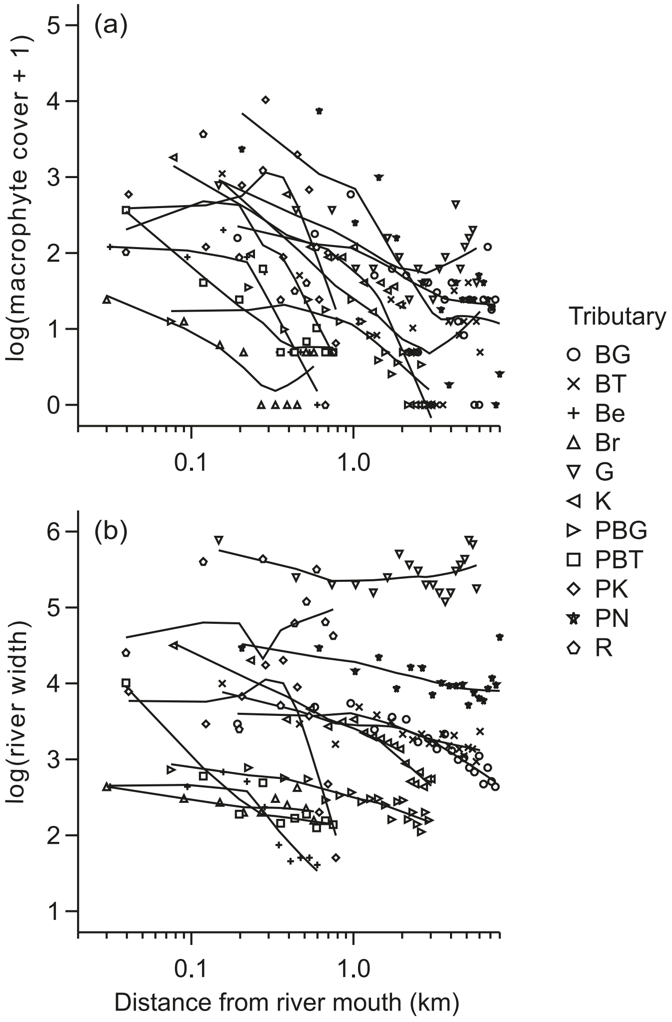
The intraclass correlations showed that most of the variation in water transparency (ICC = 0.91) and river width (ICC = 0.85) was among tributaries (Table 2). In contrast, macrophyte cover was more variable within than among tributaries (ICC = 0.27). The mixed regression analyses indicated that PectHeight, DorsDist, Barbels, and Latstripe were related significantly to water transparency; PectHeight, DorsDist, and SwimF to macrophyte cover; and PectHeight and DorsDist to river width (Table 3). None of these models required random effects for the slope. Each of the trait–environment relationships was therefore characterized by a fixed slope common to all tributaries, indicating that environmental effects were similar across tributaries.

Discussion

Among-tributary variation

In the present study, 38.7% of the total variation was among tributaries, similar to a study of fish assemblages in three tributaries of the Elbe River, Czech Republic, which also found less variation among (22.5%) than within tributaries (Humpl and Pivnička 2006). Water transparency singly

Fig. 6. Longitudinal change in (*a*) macrophyte cover (m; ln-transformed) and (*b*) river width (m; ln-transformed) for 170 sites distributed among the 11 tributaries of the Ottawa River included in this study. Be, Bélisle Brook; Br, Breckenridge Brook; G, Gatineau River; BG, Blanche à Gatineau River; PBG, Petite Blanche à Gatineau River; BT, Blanche à Thurso River; PBT, Petite Blanche à Thurso River; PN, Petite Nation River; K, Kinonge River; PK, Petite Kinonge River; R, Rouge River. The *x* axis represents distance from the mouth of the tributary (km; ln-transformed). Curves are LOWESS regressions.



accounted for a substantial fraction of the variation in assemblage structure among tributaries. Foraging performance in freshwater fish can depend critically on the match between sensory capacities and the optical environment. Water transparency has been shown to influence catchability of prey by visual foragers, such as bluegill (Luecke et al. 1990) and emerald shiner (Bonner and Wilde 2000). In floodplain lakes of the Orinoco River, Venezuela, fish with sensory adaptations to low light (e.g., well-developed lateral line system; chemical, tactile, or electric sensors) are dominant in turbid lakes, whereas fish relying on vision predominate in clear lakes (Rodríguez and Lewis 1997). The occurrence of sicklefin chub (*Macrhybopsis meeki*), which has elaborate sensory adaptations that promote foraging in turbid waters, has been shown to increase with turbidity along a longitudinal gradient in the Missouri River (Dieterman and Galat 2004).

The ecomorphological analyses pointed to links between water transparency and specific traits. The occurrence of barbels, which harbour sensitive tactile and chemical sensors, was negatively related to water transparency. This result reflects the association of brown bullhead, channel catfish (*Ictalurus punctatus*), and tadpole madtom (*Noturus gyrinus*) with turbid waters. Furthermore, the occurrence of high pectoral fins and a forward insertion of the dorsal fin, characteristic of species such as bluegill, yellow perch, golden shiner, and banded killifish, was greater in more transparent tributaries. These fins are related to maneuvering (Gibb et al. 1994; Standen and Lauder 2005), which suggests that species adept at maneuvering may rely primarily on vision to orient and forage. Eye diameter was not significantly related to water transparency in our study, contrary to previous work showing increased abundance of small-eyed species along a turbidity gradient in the upper Brazos River, Texas (Ostrand and Wilde 2002). Responses to low visibility in our study system may thus involve primarily nonvisual sensory adaptations. Alternatively, historical or phylogenetic constraints may limit the capacity for adaptive change in eye diameter.

In addition to modifying foraging behaviour, water transparency can mediate predator–prey relationships. In floodplain lakes, piscivores can shape assemblage structure by culling the most vulnerable prey species. Prey vulnerability is in turn strongly related to water transparency and to the sensory and foraging capabilities of individual species (Rodríguez and Lewis 1997). For small bluegill, a moderate increase in turbidity can reduce the risk of predation by largemouth bass in open water (Miner and Stein 1996). The ecomorphological analyses revealed a positive relationship between water transparency and the occurrence of a lateral stripe. Lateral stripes are commonly found in species that shoal and may contribute to coordinate shoal movements and confound visual predators (Krause and Ruxton 2002). Lateral stripes must lose effectiveness in these roles as visibility deteriorates, consistent with the finding that species having a lateral stripe (e.g., most *Notropis* species) were found in the most transparent tributaries.

Variation in water transparency among tributaries in this study system reflects predictable differences in sediment loading from the alluvial plain. Colonization of tributaries by species from the mainstem may not be random, but may instead reflect the sensory ecology of potential colonizers. If so, this would complement the work of Osborne and Wiley (1992), underscoring the importance of colonization processes from the mainstem to the tributaries in regulating local fish assemblages. Variation in water transparency was mostly among tributaries (ICC = 0.91), indicating that colonizers from the mainstem may be able to assess the transparency of a tributary from the confluence without exploring the tributary. Because of the importance of the optical environment to many fish species, differences in water transparency among tributaries, regardless of their origin, may contribute to structuring fish assemblages similarly in other riverine systems as well.

Within-tributary variation

Within-tributary variation in fish assemblage structure

Table 3. Intercept (*a*), slope (*b*), and *P* value for the linear mixed regressions relating ecomorphological traits to the environmental variables retained in the ordination analyses.

	Environmental variable								
	Water transparency			Macrophyte cover			River width		
Trait	*a*	*b*	*P*	*a*	*b*	*P*	*a*	*b*	*P*
Eyediam	0.051	–0.001	0.155	0.047	0.001	0.302	0.048	–0.000	0.931
Pectlength	0.167	–0.001	0.833	0.155	0.006	0.032	0.142	0.007	0.116*
Pectheight	0.188	0.007	**0.004**	0.209	0.005	**0.001**	0.192	0.007	**<0.001**
Dorsdist	0.414	–0.009	**0.018**	0.385	–0.006	**0.019**	0.402	–0.007	**0.027**
Mouth	1.030	–0.005	0.534	0.991	0.018	0.077	0.921	0.032	0.128*
Barbels	0.310	–0.053	**0.002**	0.067	0.026	0.152	–0.039	0.054	0.244
Patterns	1.322	–0.040	0.347	1.071	0.062	0.018	1.219	–0.018	0.606
Silver	0.272	0.021	0.705	0.417	–0.042	0.123	0.190	0.050	0.250
Latstripe	0.024	0.085	**0.001**	0.430	–0.041	0.087	0.221	0.046	0.067
ShapeF	1.241	0.025	0.441	1.423	–0.066	0.035	1.474	–0.058	0.253
SwimF	–0.753	0.006	0.614	–0.770	0.031	**<0.001**	–0.763	0.010	0.316

Note: The three environmental variables were ln-transformed. Bold data indicate significant relationships after adjustment by the false discovery rate procedure. With two exceptions (see footnote), all models have a random intercept and a fixed slope.

*Random intercept and slope.

was influenced mostly by longitudinal variation in macrophyte cover and river width. Many studies have shown that both fish abundance and species richness increase with macrophyte cover (e.g., Grenouillet et al. 2002; Snickars et al. 2006), presumably because vegetated habitats provide increased food availability (Grenouillet et al. 2002) and refuge against predators (Sass et al. 2006). The ecomorphological analyses indicated that macrophyte cover was positively related to the occurrence of high pectoral fins and a forward insertion of the dorsal fin, which confer maneuverability as described earlier. Maneuvering abilities related to pectoral fin size or position may confer competitive advantages when macrophyte cover is abundant. Bluegills with longer pectoral fins search for food more slowly and spend more time in vegetated habitat compared with bluegills with shorter pectoral fins, which spend more time in open-water habitat (Ehlinger 1990). Similarly, European perch (*Perca fluviatilis*) has higher foraging efficiency than European rudd (*Scardinius erythrophthalmus*) and European roach (*Rutilus rutilus*) in dense macrophyte beds, presumably because of the forward positioning of the pectoral fins in the perch (Winfield 1986). The ecomorphological analyses also indicated a positive relationship between macrophyte cover and swimming factor. Fish with a low swimming factor, such as thunniforms, are capable of strong, sustained swimming (Poff and Allan 1995). However, cruising and maneuvering abilities are usually negatively correlated (Lauder and Drucker 2004), suggesting that the negative relationship between swimming factor and macrophyte cover reflects a trade-off favouring maneuvering over cruising ability in vegetated, structurally complex environments. Macrophyte cover was linked with traits related to maneuvering but not to traits related to predator avoidance (e.g., shape factor, protective colouration), suggesting that vegetated habitat influenced community structure by allowing for efficient exploitation of abundant food resources rather than by providing refuge from predators. In contrast with transparency, variation in macrophyte cover was mostly within tributaries (ICC = 0.27), indicating that potential colonizers from the mainstem may have to enter and explore a tributary to assess macrophyte cover.

The second environmental variable associated with the within-tributary variation was river width. Although river width was positively related to macrophyte cover in the present study (median Spearman correlation = 0.62 for the 11 tributaries), the apparent effect of river width on assemblage structure is independent of macrophyte cover, which was partialled out in the ordination analysis. High pectoral fins and a forward insertion of the dorsal fin were also positively related to river width. This result agrees with the finding that maneuverers were more abundant in larger rivers in a study of 429 fish species from the Mississippi River basin (Goldstein and Meador 2004). The positive relationship between river width and maneuverability may be related to increased availability of slower flow in wider river stretches.

In conclusion, the partial analyses emphasizing among- and within-tributary components of variation in assemblage structure provided a more complete interpretation than the full analysis by showing that two distinct sets of environmental variables were associated with variation among and within tributaries. Because the full ordination combines and simultaneously represents species–environment relationships among and within tributaries, a trade-off in this representation is inevitable whenever the among- and within-tributary relationships differ. The partial ordinations also indicated that although variation in assemblage structure was greater within than among tributaries, the proportion of variation explained by environmental variables was greater among than within tributaries. These results suggest that differences in habitat features among tributaries may account for a substantial fraction of the predictable variation in assemblage structure at the watershed scale, an aspect not emphasized in previous studies of riverine fish assemblages. Our results also showed that the environmental variables most strongly associated with assemblage structure were significantly related to ecomorphological traits generally associated with foraging efficiency.

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Appendices A and B appear on the following pages.

Appendix A

Table A1. Example of effects coding for model terms in a hypothetical study of 21 sites distributed among five tributaries: three

			Tributaries (rank = 4)				Sites (rank = 5)				
Tributary	Site	$\boldsymbol{C}_1$	$\mathbf{T}_1$	$\mathbf{T}_2$	$\mathbf{T}_3$	$\mathbf{T}_4$	$\mathbf{S}_1$	$\mathbf{S}_2$	$\mathbf{S}_3$	$\mathbf{S}_4$	$\mathbf{S}_5$
1	1	1	–1	–1	–1	–1	–1	–1	0	0	0
	2	1	–1	–1	–1	–1	1	0	0	0	0
	3	1	–1	–1	–1	–1	0	1	0	0	0
2	1	1	1	0	0	0	–1	–1	0	0	0
	2	1	1	0	0	0	1	0	0	0	0
	3	1	1	0	0	0	0	1	0	0	0
3	1	1	0	1	0	0	–1	–1	0	0	0
	2	1	0	1	0	0	1	0	0	0	0
	3	1	0	1	0	0	0	1	0	0	0
4	1	1	0	0	1	0	–1	–1	–1	–1	–1
	2	1	0	0	1	0	1	0	0	0	0
	3	1	0	0	1	0	0	1	0	0	0
	4	1	0	0	1	0	0	0	1	0	0
	5	1	0	0	1	0	0	0	0	1	0
	6	1	0	0	1	0	0	0	0	0	1
5	1	1	0	0	0	1	–1	–1	–1	–1	–1
	2	1	0	0	0	1	1	0	0	0	0
	3	1	0	0	0	1	0	1	0	0	0
	4	1	0	0	0	1	0	0	1	0	0
	5	1	0	0	0	1	0	0	0	1	0
	6	1	0	0	0	1	0	0	0	0	1

Note: The table includes coefficients for a constant term, $\boldsymbol{C}$ (a column vector of ones), which is included in all models, and three matrices of variables, taries and sites ($\mathbf{T}\cdot\mathbf{S}$). All of the matrices have full rank. Design matrices for different models can be constructed as combinations of the constant vector $\boldsymbol{C}$ among tributaries, includes the five columns associated with terms $\boldsymbol{C}$ and $\mathbf{T}$. The design matrix for model $\boldsymbol{C} + \mathbf{T} + \mathbf{S} + \mathbf{T}\cdot\mathbf{S}$ includes all 21 columns, has full tributaries with three sites each and two tributaries with six sites each.

Tributaries × Sites interaction (rank = 11)										
$\mathbf{T}\cdot\mathbf{S}_1$	$\mathbf{T}\cdot\mathbf{S}_2$	$\mathbf{T}\cdot\mathbf{S}_3$	$\mathbf{T}\cdot\mathbf{S}_4$	$\mathbf{T}\cdot\mathbf{S}_5$	$\mathbf{T}\cdot\mathbf{S}_6$	$\mathbf{T}\cdot\mathbf{S}_7$	$\mathbf{T}\cdot\mathbf{S}_8$	$\mathbf{T}\cdot\mathbf{S}_9$	$\mathbf{T}\cdot\mathbf{S}_{10}$	$\mathbf{T}\cdot\mathbf{S}_{11}$
1	1	1	1	1	1	1	1	0	0	0
–1	–1	–1	–1	0	0	0	0	0	0	0
0	0	0	0	–1	–1	–1	–1	0	0	0
–1	0	0	0	–1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0
0	–1	0	0	0	–1	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0
0	0	–1	0	0	0	–1	0	–1	–1	–1
0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	0	0	1
0	0	0	–1	0	0	0	–1	0	0	0
0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0

constructed as effects coding for tributaries (**T**), sites within tributaries (**S**), and the interaction between tribu-
with the **T**, **S**, and **T·S** matrices. For example, the design matrix for model ***C*** + **T**, which accounts for variation
rank, and accounts for all the variation in assemblage structure because its rank equals the number of sites.

Appendix B

Table B1. Mean number per site and percentage of the total number of fish for 49 fish species in the 11 tributaries of the Ottawa River included in this study.

Family	Scientific name	Common name	Code	Mean	Percentage
Atherinopsidae	*Labidesthes sicculus*	Brook silverside	LabSic	0.03	0.03
Catostomidae	*Carpiodes cyprinus*	Quillback	CarCyp	0.05	0.04
	Catostomus commersonii	White sucker	CatCom	0.61	0.53
	Moxostoma anisurum	Silver redhorse	MoxAni	0.06	0.05
	Moxostoma carinatum	River redhorse	MoxCar	0.01	0.01
	Moxostoma macrolepidotum	Shorthead redhorse	MoxMac	0.06	0.05
Cyprinidae	*Cyprinus carpio*	Common carp	Cypcar	0.04	0.03
	Hybognathus hankinsoni	Brassy minnow	HybHan	0.01	0.01
	Hybognathus nuchalis	Mississippi silvery minnow	HybNuc	3.16	2.76
	Luxilus cornutus	Common shiner	LuxCor	1.14	0.99
	Notemigonus crysoleucas	Golden shiner	NotCry	2.40	2.09
	Notropis atherinoides	Emerald shiner	NotAth	8.36	7.28
	Notropis bifrenatus	Bridled shiner	NotBif	0.01	0.01
	Notropis heterodon	Blackchin shiner	NotHed	0.02	0.02
	Notropis heterolepis	Blacknose shiner	NotHel	0.04	0.04
	Notropis hudsonius	Spottail shiner	NotHud	1.26	1.10
	Notropis rubellus	Rosyface shiner	NotRub	0.02	0.02
	Cyprinella spiloptera	Spotfin shiner	CypSpi	0.52	0.46
	Notropis stramineus	Sand shiner	NotStr	0.04	0.03
	Notropis volucellus	Mimic shiner	NotVol	2.98	2.60
	Pimephales notatus	Bluntnose minnow	PimNot	1.39	1.21
	Pimephales promelas	Fathead minnow	PimPro	0.02	0.02
	Rhinichthys cataractae	Longnose dace	RhiCat	0.01	0.01
	Semotilus atromaculatus	Creek chub	SemAtr	0.01	0.01
	Semotilus corporalis	Fallfish	SemCor	2.20	1.92
Esocidae	*Esox lucius*	Northern pike	EsoLuc	0.35	0.30
	Esox masquinongy	Muskellunge	EsoMas	0.16	0.14
Fundulidae	*Fundulus diaphanus*	Banded killifish	FunDia	0.12	0.10
Umbridae	*Umbra limi*	Central mudminnow	UmbLim	1.04	0.90
Lepisosteidae	*Lepisosteus osseus*	Longnose gar	LepOss	0.05	0.04
Hiodontidae	*Hiodon tergisus*	Mooneye	HioTer	0.15	0.13
Centrarchidae	*Ambloplites rupestris*	Rock bass	AmbRup	8.36	7.28
	Lepomis gibbosus	Pumpkinseed	LepGib	17.40	15.20
	Lepomis macrochirus	Bluegill	LepMac	5.21	4.53
	Micropterus dolomieu	Smallmouth bass	MicDol	0.49	0.43
	Micropterus salmoides	Largemouth bass	MicSal	5.99	5.22
	Pomoxis nigromaculatus	Black crappie	PomNig	23.91	20.82
Percidae	*Etheostoma nigrum*	Johnny darter	EthNig	2.29	1.99
	Percina caprodes	Logperch	PerCap	2.19	1.91
	Percina copelandi	Channel darter	PerCop	0.12	0.11
	Perca flavescens	Yellow perch	PerFla	17.91	15.60
	Sander canadensis	Sauger	SanCan	0.18	0.16
	Sander vitreus	Walleye	SanVit	0.15	0.13
Sciaenidae	*Aplodinotus grunniens*	Freshwater drum	AplGru	0.04	0.03
Percopsidae	*Percopsis omiscomaycus*	Trout-perch	PerOmi	2.01	1.75
Petromyzontidae	*Ichthyomyzon unicuspis*	Silver lamprey	IchUni	0.01	0.01
Ictaluridae	*Ameiurus nebulosus*	Brown bullhead	AmeNeb	2.23	1.94
	Ictalurus punctatus	Channel catfish	IctPun	0.01	0.01
	Noturus gyrinus	Tadople madtom	NotGyr	0.03	0.03

Note: A total of 19 518 fish were captured.